

The Archaeogastropoda A clade, a grade or what else?¹

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Abstract: The classic concept of Thiele's Archaeogastropoda includes the Docoglossa (now Patellogastropoda), Neritacea (now Neritimorpha), Cocculinacea (now Cocculiniformia), Zeugobranchia and Trochacea (now Vetigastropoda). The recent discovery of many new archaeogastropod groups mainly from deep waters, and in particular from the hydrothermal vent habitat, necessitates a reevaluation of the taxon. Archaeogastropoda can still be clearly defined by protoconch characters and by the diagnostic streptoneurous and hypoathroid nervous system (close association of pleural and pedal ganglia). This definition also includes the Neritimorpha and the architaenioglossate groups. The amount of convergence is very high among archaeogastropods, most characters of advanced gastropods occurred several times in parallel in evolution.

As in Thiele's time, the taxon "Archaeogastropoda" is regarded as the basic gastropod stem group and should be classified as a paraphyletic taxon. Whether this stem group gave rise to a single or two lines of higher gastropods is still a matter of debate.

The taxon Archaeogastropoda was introduced by Thiele (1925) and cemented by the author in his famous "Handbuch der Systematischen Weichtierkunde" (Thiele, 1929). Five subgroups were included, namely the "Stirps" Zeugobranchia (those with two gills, now included in Vetigastropoda), the Patellacea or Docoglossa (now also called Patellogastropoda), the Trochacea (now included in Vetigastropoda), the Neritacea (now Neritimorpha), and the Cocculinacea (now Cocculiniformia). Although quite weakly defined - there was not a single diagnostic character given - the use and value of the taxon Archaeogastropoda has not been seriously questioned until very recent times [see Hickman (1988) for detailed historical review].

The first reason to question the use of Archaeogastropoda is due to the many recent discoveries of new archaeogastropod species and groups from the deep-sea, in particular but not exclusively from the strange habitat of the hydrothermal vents. Starting with the enigmatic *Neomphalus fretterae* McLean, 1981, these now include several groups, for which various ranks between genus and order have been proposed (e.g. Hickman, 1984; Marshall, 1988; McLean, 1988, 1989a, b, 1990a, b, 1992; Warén and Bouchet, 1989; Warén, 1989, 1991, 1992; Beck, 1992a, b). Anatomical investigations of these forms (e.g. Fretter, 1988, 1989, 1990; Haszprunar, 1989a, b) as well as of other long-named archaeogastropods such as the Cocculiniformia [see

Haszprunar (1988a, b) for review, also 1992c] show that at least certain archaeogastropods are by far more advanced and more variable than previously thought. Obviously the assumption is no longer valid that Archaeogastropoda describes a specific level of organization, as it may be holophyletic, paraphyletic or polyphyletic. Consequently, the question arises: "What is an archaeogastropod?" or better: "Is it possible to define a taxon Archaeogastropoda and what status has that taxon?"

A second reason to question the validity of the taxon Archaeogastropoda is based on the cladistic point of view. Most cladists argue to use in phylogenetic systems only monophyletic (*sensu stricto*, i.e. holophyletic), i.e. groups with a common ancestor, which include all descendants of that ancestor (e.g. Hennig, 1966; Wiley, 1981). Because most authors regard Archaeogastropoda in the sense of Thiele (1929) as a paraphyletic (e.g. Haszprunar, 1988b; see also below) or even as a polyphyletic (e.g. Hickman, 1988), the taxon should no longer be used any more according to that view. In contrast, the author (Haszprunar, 1986, 1988b) has argued to retain paraphyletic taxa in classifications, if (and only if) (1) they are qualified as such and (2) the relationships between taxa are expressed exactly.

In this paper various characters, which have been used to define the taxon Archaeogastropoda, or which are considered primitive for gastropods in general, will be analyzed with respect to homology questions and distribution.

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After that the status and validity of the taxon Archaeogastropoda will be discussed.

HOW TO DEFINE ARCHAEOGASTROPODA? – CHARACTER ANALYSIS

GENERAL REMARKS

In the following, "Archaeogastropoda" is used in the sense of Haszprunar (1988b), including the Patellogastropoda (i.e. Docoglossa, including the Neolepetopsidae, the former "hot-vent group C"), Cocculiniformia, Neritimorpha, *Melanodrymia*, Peltospiroidea (formerly "hot-vent group A"), Neomphaloidea, Vetigastropoda (including also the Seguenzioidea, see below), and the architaenioglossate groups (Cyclophoroidea, Ampullarioidea). Fossil groups could be added, if shell characters suggest their archaeogastropod nature (see below).

The term "character analysis" is used here in the sense that homology questions as well as distribution patterns are discussed. To a certain extent this has been done already earlier (Haszprunar, 1988b), nevertheless I think it is justified to present an updated review: Firstly, there are several new groups to be considered, secondly, certain characters (e.g. heterostrophy) have been differently interpreted by other authors, and finally, certain new characters (e.g. developmental timing) have been proposed meanwhile.

TELEOCONCH

It is obvious that shell shape cannot be used to define Archaeogastropoda, because all types of shell morphology are found. However, so-called "symmetrical" limpets, which do not show any coiling of the juvenile teleoconch, are not found in any other gastropod group. Confusion of symmetrical limpets with the neopilinids (Monoplacophora) can be ruled out if (1) the shell apex is posterior; or (2) a deformed protoconch is present (see below); or (3) muscle scars are visible; or (4) shell structure is considered. The presence of nacre is restricted to the archaeogastropod grade (among Gastropoda), although many groups have lost or replaced it secondarily.

Whereas a shell slit/hole(s) is characteristic for zeugobranch groups (Scissurelloidea, Fissurelloidea, Haliothioidea, and Pleurotomarioidea), it is not diagnostic at all, since shell slits are also found in Siliquariidae (Cerithioidea) and many Bellerophonitida, the gastropod nature of which is still questionable [see Haszprunar (1988b) for recent review].

PROTOCONCH

Scanning electron microscopy has revealed many new characters useful for gastropod systematics. In particu-

lar, protoconch features (Fig. 1) are very useful to define distinct groups. According to the information available, four types of protoconch formation are typical for archaeogastropods:

(1) In the Patellogastropoda, the embryonic shell (i.e. protoconch I, mineralized at once by the shell gland) is usually not really coiled but more or less bent [e.g. Bandel, 1982 (figures labeled as *Cocculina reticulata* Verrill, 1884 (p. 35, Abb. 26; Tafel 8, Figs. 4, 5, 9) and *Cocculina* cf. *spinigera* (p. 36, Abb. 27A; Tafel 8, Figs. 3, 6, 8) very probably show lepetids rather than cocculinids. Compare with SEM-photos of cocculinid limpets in Marshall (1986); Warén, 1988; Fig. 1A]. Depending on the amount of yolk the embryonic shell may or may not be symmetrical (see Bandel, 1982). After metamorphosis the embryonic shell is lost together with the early teleoconch after the formation of a distinct septum leaving a characteristic scar (Smith, 1935; Bandel, 1982; Warén, 1988). Very often the axes of the embryonic and adult patellogastropod shell form a characteristic angle (e.g. Thompson, 1912). This angle has been interpreted as reminiscent of a coiled ancestor by Lindberg (1988). In this case [but see contrary arguments in Haszprunar (1988b: 370-372)], such an ancestor probably had an hyperstrophic rather than an orthostrophic teleoconch, (see legend of Fig. 1 for definitions) judging from the orientation of the axes.

(2) In the lepetelloid limpets (Choristellidae show a vetigastropod-like protoconch, see below) the apex of the embryonic shell is fused in a very characteristic way with the teleoconch, resulting in lateral pouches (cf. Marshall, 1986; Fig. 1B).

(3) The neritimorph condition (Fig. 1C) is unique among the archaeogastropods in showing a true, multispiral larval shell (i.e. protoconch II, formed and mineralized successively by the mantle margin). As outlined by Bandel (1982, 1992) this type of larval shell is diagnostic for the Neritimorpha and can be used to infer close relationships between this group and the extinct Platyceratoidea.

(4) The majority of archaeogastropods show the so-called "trochoid" condition, in which the embryonic shell is immediately followed by the teleoconch. The morphology of the embryonic shell is highly variable (e.g. Hickman, 1992: fig.5; Fig. 1D,E,F) and could well be used to diagnose minor taxa. In contrast, caenogastropods have orthostrophic larval shells (Fig. 1G-H), and heterobranchs show hyperstrophic larval shells (Fig. 1I-K), although the condition may be cryptic in the case of lecithotrophic development.

Recently, Hadfield and Strathmann (1990) described "hyperstrophic" protoconchs resp. "heterostrophy" (see legend of Fig. 1 for definitions of terms) of certain trochoid species (see also Hickman, 1992: fig. 5L). However, the term "heterostrophy" describes a relationship

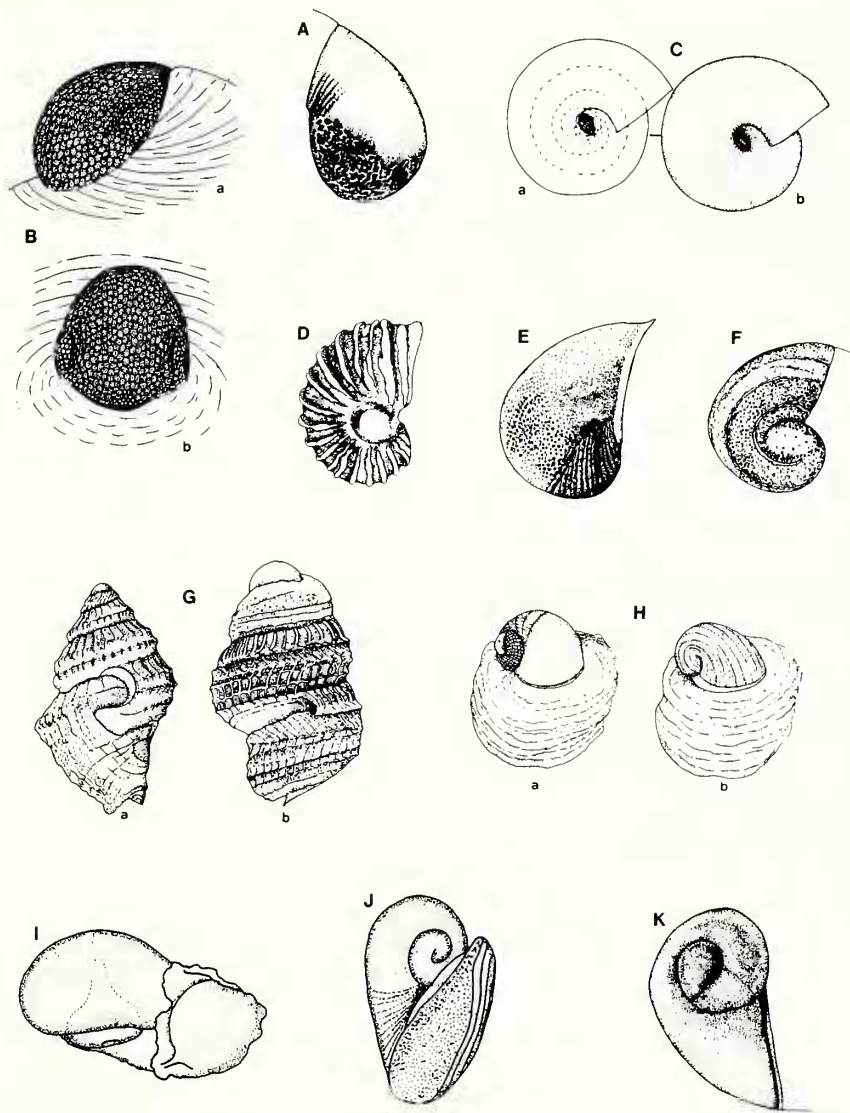


Fig. 1: Protoconchs of selected gastropods. **A.** Patellogastropoda-Lepetidae (200-800 m off SE-coast of USA). The embryonic shell (lateral view from the left) is bulbous, the deformation is not planispiral in this case ("*Cocculina reticulata*" from Bandel, 1982: fig. 26). **B.** Cocculiniformia-Pseudococculinidae: *Mesopelex zelandica* Marshall, 1986: Embryonic shell (about 135 μm wide and 210 μm long) with subreticulate sculpture from (a) lateral right and from (b) anterior showing bilateral symmetry (after SEM-photos of Marshall, 1986: figs. 10C, D). **C.** Neritimorpha-Neritidae: *Smaragdia* sp. (Red Sea): Larval shell in (a) transparent to show whorl contours, in (b) external view (from Bandel, 1982: fig. 73). **D.** Vetigastropoda-Scissurellidae: *Sinezona* sp. (Gmelin, 1791) (Canary Islands): Embryonic shell with strong axial ribs (from Bandel, 1982: fig. 20). **E.** Vetigastropoda-Fissurellidae: *Fissurella angusta* Woodring, 1928: Embryonic shell with apertural ridge and sculpture caused by deformation during torsion (from Bandel, 1982: fig. 21). **F.** Vetigastropoda-Trochidae: *Microgaza vetula* L., 1767: Embryonic shell with a mixture of spiral ribs and tubercles as sculpture (from Bandel, 1982: fig. 18). **G.** Coiled Caenogastropoda: (a) *Thais haemostoma* (Muricoidea); (b) *Cerithium litteratum* (Born, 1778) (Cerithioidea): Embryonic and larval shell show different sculptures because of planktotrophic development (from Bandel, 1982: fig. 87). **H.** Caenogastropod limpets (Hipponicoidea): (a) *Hipponix conicus* (Schumacher, 18417): Embryonic and larval shell show different sculpture; (b) *Hipponix antiquatus* (L., 1767): Embryonic and larval shell cannot be distinguished by sculpture (from Bandel, 1982: fig. 82). **I.** Allogastropoda-Architectonicidae: *Philippia krebsii* (Mörch, 1875): The larval shell is hyperstrophic¹⁾, whereas the adult shell starts orthostrophically¹⁾. Note anastrophic²⁾ relationship between larval and adult shell (after Robertson, 1974 from Haszprunar, 1985b: fig. 1c). **J.** Opisthobranchia-Acteonoidea: *Acteon tornatilis* L., 1758: The larval shell is hyperstrophic¹⁾, whereas the adult shell starts orthostrophically¹⁾. Note heterostrophic (sensu lato)²⁾ relationship between larval and adult shell [after Thorson, (1946) from Haszprunar (1985b: fig. 1d)]. **K.** Pulmonata-Siphonariidae: *Williamia krebsii* (Mörch, 1877): The embryonic shell can be clearly distinguished from the hyperstrophic¹⁾ larval shell (from Bandel, (1982: fig. 83).

¹⁾ "Orthostrophy" and "hyperstrophy" refer to the relationship between the orientation (left or right-handed) of a helicoid (larval or adult) shell and the orientation of the soft body. If shell and soft body are equally handed (regular gastropods, but also triphorids) this is called "orthostrophic", if they are differently handed (e.g. larval heterobranchs, neotenic Euthecosomata, also the adult ampullariid *Lanistes*), it is called "hyperstrophy".

²⁾ "Heterostrophy" (sensu lato) means the different orientation of the axes of the larval and the adult shell. If the angle of axes is about 90° this is called "heterostrophy sensu stricto", if the angle is about 180° this is called "anastrophy".

between a larval shell (see Fig. 1 for definitions) and the teleoconch. In this sense it was taken by Robertson (1985), Haszprunar (1985, 1988b), Bandel (1982, 1988b, 1992), and Ponder (1991). The formation and mode of coiling of an "hyperstrophic" embryonic shell are the results of an entirely different process compared with a hyperstrophic larval shell (Bandel, 1982: 27-36; Hickman, 1992; Warén and Bouchet, 1993: 49). Therefore the "heterostrophy" of these trochoids does not corroborate the concept of heterostrophy respectively of the hyperstrophic larval shell as a basic synapomorphy of heterobranch gastropods (Robertson, 1985; Haszprunar, 1985, 1988b; Ponder, 1991). However, the presence of hyperstrophic-like embryonic shells among archaeogastropods supports the statement made by Haszprunar (1988b) that torsion and the mode of shell coiling are primarily independent features.

(5) All the above mentioned characters concern marine species. Freshwater and terrestrial gastropods generally show modifications in shell ontogeny. Whereas nearly nothing is known concerning shell ontogeny of cyclophoroids, the shell formation of ampullariids has been studied in some detail (e.g. Demian and Yousif, 1973a, b; Honegger, 1974; Lehmann, 1992). In particular Lehmann (1992) pointed out major differences between ampullariid and archaeogastropod (including neritimorph) shell development. According to his results it appears more likely that the Ampullariidae have reached the caenogastropod level concerning shell formation.

Summing up, protoconch characters enable one to distinguish clearly certain groups of (marine) archaeogastropods, caenogastropods and heterobranchs. It also shows that diagnostic features exist to define some fossil archaeogastropod groups, where protoconch data are available. This has been already applied to split up such "lumping pots" as the extinct "Euomphalacea" (e.g. Bandel, 1988a) or the recent "skeneimorphs" (e.g. Warén, 1992).

SHELL MUSCLES

As reviewed earlier (Haszprunar, 1985c, 1988b), ontogenetic as well as anatomical investigations show that in many archaeogastropods the adult shell muscles are paired, whereas they are unpaired in caenogastropods and heterobranchs. However, certain archaeogastropods also show the unpaired condition with a left muscle only (e.g. *Neomphalus*, many trochoids)

MANTLE CAVITY

The archaeogastropod mantle cavity is usually fully torted, having its opening anteriorly situated. Certain lepetelloidean limpets show a somewhat detorted orientation of the rectal-nephridial complex, whereas *Neomphalus* is unique in showing an hypertorted condition.

It is generally accepted that a paired set of pallial organs (osphradia, ctenidia, hypobranchial glands) is the primitive condition among the gastropods. Indeed, retention of this character state is found only within the archaeogastropod grade, although there are many groups that have lost one or more of the right-side organs.

CTENIDIA

As outlined elsewhere (Haszprunar, 1988b: 377-383) gastropod ctenidia are highly variable. The only gastropod gill-type, which is exclusively found within the Archaeogastropoda, is bipectinate and supplied by skeletal rods. Hickman (1988) recently proposed that this character should be diagnostic for a restricted use of "Archaeogastropoda" equivalent to Vetigastropoda. However, the same character set is found in *Neomphalus* and certain coiled peltospiroids (but not in *Melanodrymia*; see Haszprunar, 1989b), whereas on the other hand certain vetigastropods such as *Temnocinclis*, *Temnozaga*, *Fissurisepta*, many skeneids, or seguenziids) show monopectinate gills (see Cowan, 1969; Haszprunar, 1988b, 1989a, unpubl. data).

CIRCULATORY AND EXCRETORY SYSTEM

Comparable with the conditions of the pallial organs, the retention of two auricles (diotocard condition) or two kidneys is restricted to archaeogastropods. As demonstrated by the lepetodriloid and trochoid vetigastropods the loss of the right gill does not necessarily imply the loss of the right auricle. Again, however, many forms have independently reached the monotocardian or single (left) kidney condition of higher gastropods. Parallel events of loss are probable also with respect to the penetration of the pericardium by the rectum.

GENITAL SYSTEM, GAMETES, AND REPRODUCTION

Archaeogastropods are usually considered to be "primitive" with respect to reproduction in showing free (ectaquatic) fertilization. This is correlated with the so-called "primitive type" of spermatozoa, which (among gastropods) is indeed restricted to archaeogastropods. However, entaquatic (in the female's mantle cavity) or internal fertilization occurs frequently among archaeogastropods, in particular (1) in very small forms; (2) in deep-water species, including those from the hydrothermal vent habitat; (3) in freshwater or terrestrial groups. It should be stressed that in fact all so-called "advanced" conditions concerning molluscan reproduction such as internal fertilization, paraspermatozoa, spermatophores, copulatory

organs, receptacula, or brooding, are found in various archaeogastropod groups. Even within the Trochoidea, developmental data (e.g. time of hatching, planktonic versus non-planktonic mode of development) vary considerably (Hickman, 1992). Concerning reproduction, Archaeogastropoda is certainly not a grouping of the same level of organization.

Recently, Jamieson (1991) pointed out for teleost fishes that the "primitive type" of spermatozoa (respectively ectaquatic fertilization) is probably an advanced feature in that group. The same conclusion has been reached for solitary ascidians (e.g. Franzén, 1992). Considering early gastropods to be very small animals (Haszprunar, 1988b, 1992a), entaquatic fertilization (by sperm of the "primitive type") could be the more primitive archaeogastropod condition.

CLEAVAGE PATTERN

Most recently Van den Biggelaar (1993) paid attention to distinct differences between archaeogastropods and higher groups (Caenogastropoda and Heterobranchia) in the spatiotemporal cleavage pattern.

(1) Whereas in archaeogastropods (*Patella vulgata* L., 1758, *Haliotis tuberculata* L., 1758 and *Gibbula magus* (L., 1767) have been investigated) the mesentoblast (i.e. the 4d—cell) is formed at the transition of the 63- into the 64-cell stage, this occurs already at the transition of the 24- into the 25-cell stage in caenogastropods (e.g. *Littorina*, *Crepidula*, *Ilyanassa*), Opisthobranchs (e.g. *Haminoea*, *Aplysia*, *Doris*), and pulmonates (e.g. *Physa*, *Lymnaea*, *Biomphalaria*). Because the formation of the mesentoblast occurs even later (72-73 cell stage) in the Polyplacophora (e.g. see Heath, 1912), the archaeogastropod condition is considered as plesiomorphic.

(2) In the gastropods there is a distinct trend to retard the formation of the first quartet cells and the formation of the prototroch not only in relation to the development of the mesentoblast, but also in relation to absolute cell numbers. In *Patella*, the trochoblasts already divide between the 32-cell and the 40-cell stage and thus clearly before the formation of the mesentoblast. In *Haliotis*, this occurs between the 52-cell and 60-cell stage; in *Gibbula*, between the 55-cell to 64-cell stage, thus nearly parallel with the formation of the mesoentoblast. In caenogastropods the first division of the trochoblasts follows the formation of the mesentoblast, whereas in opisthobranchs the formation of the first quartet cells is even more retarded.

(3) The acceleration of the formation of the prototroch in caenogastropods, opisthobranchs and pulmonates is further associated with a considerably smaller number of cells, which build up the prototroch. This is probably corre-

lated with the fact that the trochophore stage is free in *Patella*, partly free in *Haliotis* and *Gibbula*, and within the egg-capsule in higher gastropods. In the latter groups the prototroch is further transformed to the velum, which is built up by very many cells. It is unknown at present whether the trochoblasts are dividing again after differentiation or whether cells of different source are included in the velum (Van den Biggelaar, pers. comm.).

Although the present number of investigated species is still very low (e.g. no data on marine Neritoidea or allogastropods), such data on the spatiotemporal pattern of development might become very useful for phylogenetic purposes.

RADULA AND SUPPORTING STRUCTURES

The main basis of Thiele's Archaeogastropoda was the uniting of groups with a rhipidoglossate or docoglossate radula. However, the docoglossate (stereoglossate) condition, i.e. simple rasping without longitudinal bending of the radular membrane and magnetite in the lateral teeth, is likewise found in neopilinids and chitons. Moreover, the recent discovery of valvatoideans (pers. obs. on anatomy; sperm data from J.M. Healy, 1993b) with rhipidoglossate radula (but with entirely different buccal apparatus, pers. obs.), the Hyalogyrinidae (Warén and Bouchet, 1993; Warén *et al.*, 1993) omits also the second type as a simple diagnostic character for Archaeogastropoda. In addition, there are several archaeogastropod groups, in particular the Cocculiniformia (e.g. Hickman, 1983) but also several trochoid groups such as Trochaclidinae or Thysanodontinae (cf. Hickman and McLean, 1990), the radula of which do not fit any of the standard categories.

The presence of several pairs of radular cartilages is restricted to the Archaeogastropoda. Certain archaeogastropods and caenogastropods in general have a single pair or none; Heterobranchia lack true cartilages, some have secondary ones. The combination "docoglossate or rhipidoglossate radula with massive cartilages" is restricted to archaeogastropods, however.

Most archaeogastropods are provided with a so-called radular diverticulum (cf. Haszprunar, 1988: 392), which is lacking only in the architaenioglossate groups.

ALIMENTARY TRACT

As outlined elsewhere (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988b) the presence of oesophageal pouches, which can be simply structured or papillate, is restricted to Archaeogastropoda (among Gastropoda). The same is true for the so-called "anterior loop" of the intestine. In both cases, however, certain

archaeogastropods have reached independently the advanced stage.

NERVOUS SYSTEM

Pedal cords are common among archaeogastropods, but are also present in certain caenogastropods such as *Lavigeria* (Cerithioidea) (Moore, 1899 as *Nassopsis*) or in the Cypraeidae (e.g. see Riese, 1930). Therefore the character cannot be used to define Archaeogastropoda. The presence of a labial commissure is restricted to archaeogastropods, again however, many members have lost it in parallel to caenogastropods and heterobranchs.

As stated repeatedly (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a, b) the condition of a hypoathroid cerebropedal ring (i.e. pleural and pedal ganglia being close together) is the only character that is present in all archaeogastropods including the architaenioglossate groups. In the Viviparidae alone the hypoathroid condition is restricted to the left side, whereas the right side is epiathroid (close up of cerebral and pleural ganglia). This condition is independent of habitat (marine, freshwater, terrestrial), habit (mode of nourishment), or other modifications of the central nervous system (see above). In contrast, all caenogastropoda and primitive heterobranchs show an epiathroid condition.

The hypoathroid condition is also found in certain euthyneuran (i.e. osphradial ganglion at the right side; cf. Haszprunar, 1985b, 1988b) groups such as Aplysiomorpha or Gymnosomata (cf. Hoffmann, 1932-39) or in the Eupulmonata (Trimusculoidea, Ellobioidea, and most Stylommatophora; cf. Haszprunar and Huber (1990) for review). Therefore, I have defined the Archaeogastropoda by a "streptoneurous and hypoathroid nervous system" (Haszprunar, 1988b). Moreover, the hypoathroid-like conditions of euthyneurans differ in two fundamental aspects from that of the Archaeogastropoda:

(1) Several authors agree that in the euthyneurans the original pleural ganglion is split off into the pleural *sensu stricto* and so-called parietal ganglion (Regondaud *et al.*, 1974; Brace, 1977; Schmekel, 1985, Haszprunar, 1988b; Haszprunar and Huber, 1990). Usually the hypoathroid condition of euthyneurans concern the pleural ganglia alone, whereas the parietal ganglia are not included, but are fused with the suboesophageal or supraoesophageal ganglion.

(2) So far known the hypoathroid condition of euthyneurans is a secondary phenomenon, because during ontogeny an epiathroid condition respectively a common cerebropleural anlage is primarily established as in caenogastropods or in epiathroid heterobranchs. This is well documented in *Aplysia* (e.g. Kandel *et al.*, 1980; Jacob, 1984; Fig. 2E-F), in the Ellobiidae (Ruthensteiner,

1991, 1992; Fig. 2G-H), and in the Stylommatophora (e.g. Henchmann, 1890). In contrast, the anlage of the pleural ganglion is always close to the pedal ganglion in the Archaeogastropoda. This has been described in *Patella* (Smith, 1935), *Haliotis* (Crofts, 1937; Barlow and Truman, 1992; fig. 2A-B), *Theodoxus* (Ruthensteiner, 1991: 72), *Ampullarius* (Honegger, 1974), and *Marisa* (Demian and Yousir, 1975; fig. 2C-D). The single exception is again *Viviparus* (left side hypoathroid, right side epiathroid as adults; see above), for which Andersen (1924) described a common cerebropleural anlage as in caenogastropods or heterobranchs.

Most recently, Page (1992a, b) claimed an hypoathroid condition in a dendronotoid nudibranch *Melibe leonina* (Gould, 1852). Her results are based on fine-structural studies and include: (1) the pleurals originate from a post-trochal placode as in archaeogastropods; (2) the pleurals are situated in front of the pedal ganglia; (3) the pleurals are connected to the labial lobe of the cerebral ganglia. Nevertheless, the presented interpretation causes serious problems: (1) the results are in direct contrast to all previous ones on neurogenesis in nudibranchs (e.g. Thompson, 1958, 1962; Tardy, 1970, 1974); (2) Her "labial lobe" of pyramidellids ("sensory lobe" of Fretter and Graham, 1949) is a rhinophoral ganglion [pers. obs.; see also Haszprunar and Huber (1990) for discussion], and it is likely that the same statement can be made about the "labial lobe" of *Melibe*; (3) *Melibe leonina* (Gould, 1852) would be the only gastropod (mollusc), in which the visceral loop does not start from the pleural ganglia, but directly from the cerebral ganglia. Moreover, there is no connection between the labial lobe and the pleural ganglia in any other gastropod; (4) the "pleural" ganglia of *Melibe* strongly resemble the so-called propodal ganglia of *Onchidoris bilamellata* L., 1767, which are likewise connected with the cerebral ganglia (Chia and Koss, 1989). All these arguments suggest that the interpretation of Page (1992a, b) is incorrect. Nevertheless, modern neuroanatomical trace methods such as antibody-staining or cobalt-filling [cf. Heimer and Zaborszky (1989) for review] are necessary to finally accept or reject this proposal. However, even if the interpretation of Page (1992 a, b) would be correct, the conditions of *Melibe* are clearly not directly comparable with those of the Archaeogastropoda and do not influence the validity of the hypoathroid nervous system as a diagnostic character of the Archaeogastropoda.

SENSE ORGANS

Eyes lacking a cornea are restricted to the Archaeogastropoda, although several groups have developed closed eyes. A subradular organ is found only in certain archaeogastropods. Epipodial tentacles also occur in certain

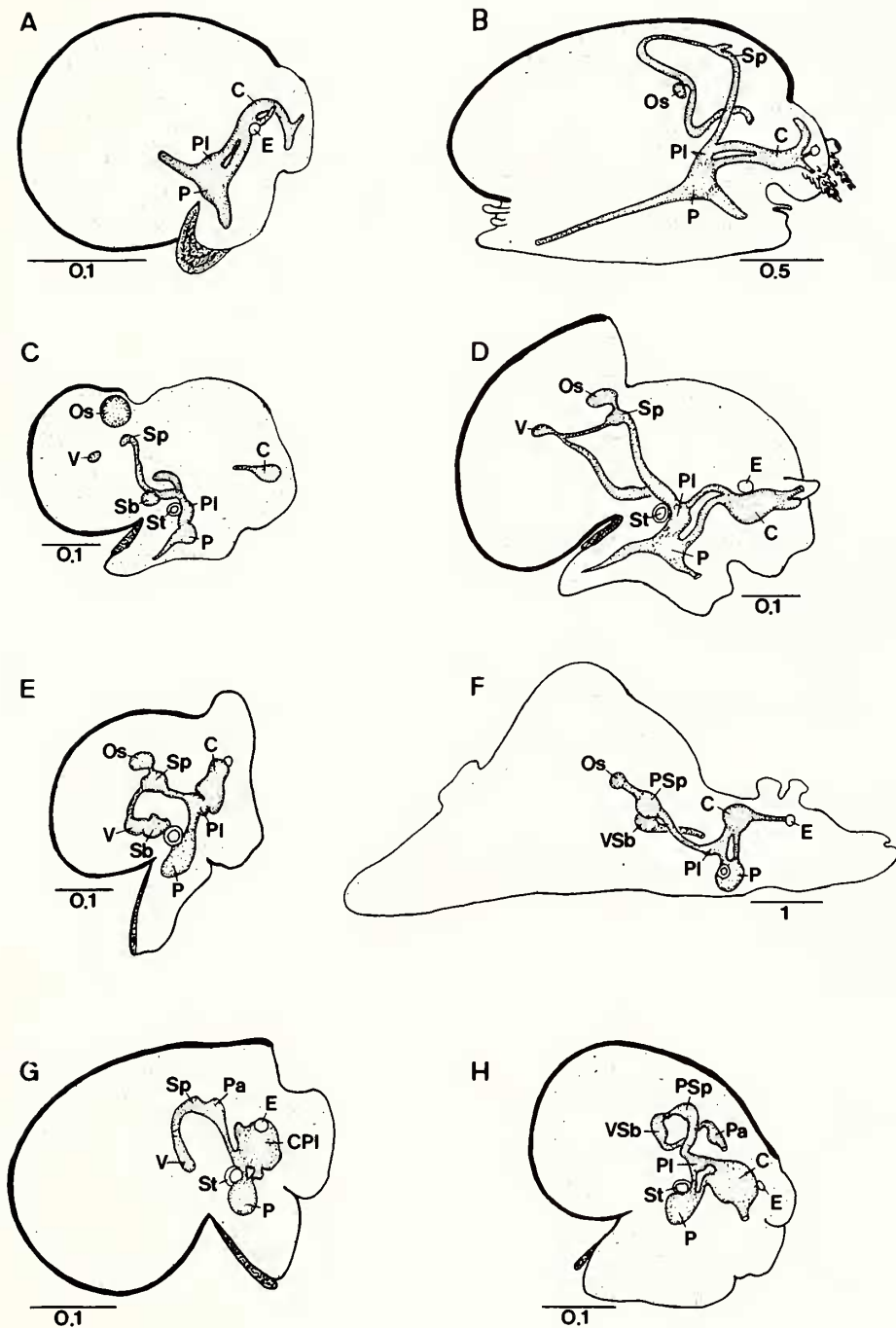


Fig. 2. Comparative view of ontogenesis of the nervous system in selected gastropods to demonstrate primary versus secondary hypoathroid conditions. Scale bars in millimeter. (C - cerebral ganglion; CPI - cerebropleural ganglion; E - eye; Os - osphradial ganglion; P - pedal ganglion, Pa - parietal ganglion; P1 - pleural ganglion; PSp - fused parietal and supraoesophageal ganglion; Sb - suboesophageal ganglion; Sp - supraoesophageal ganglion; St - Statocyst; V - visceral ganglion; VSb - fused visceral and suboesophageal ganglion). **A-B.** *Haliotis tuberculata* L., 1758 (Vetigastropoda - Haliotioidea) with hypoathroid nervous system from the beginning. A. 3 days old veliger. B. About 2 months old post-veliger (modified after Crofts, 1937). **C-D.** *Marisa cornuarietis* (L., 1758) (Architaenioglossa - Ampullarioidea) with hypoathroid nervous system from the beginning. C. Embryo stage VIII (90 hours at 25-30°C respectively 3 days at 15-20°C). D. Embryo stage X (5 days at 25-30°C respectively 14 days at 15-20°C) (modified after Demian and Yousif, 1975). **E-F.** *Aplysia californica* Cooper (Opisthobranchia - Aplysioidea): E. 3 weeks old veliger with epiathroid condition. F. 2 months old juvenile with pleural ganglion in intermediate position (adults are fully hypoathroid) (modified after Kandel *et al.*, 1979). **G-H.** *Ovatella (Myosotella) myosotis* (Draparnaud, 1804) (Pulmonata - Ellobioidea). G. Veliger 12 days old with fused cerebropleural ganglion. H. Hatchling about 21 days old with pleural ganglion in intermediate position (adults are fully hypoathroid, (modified after Ruthensteiner, 1991).

caenogastropods such as *Alaba* or *Litiopa* (Cerithioidea) (Houbrick, 1987), epipodial sense organs appear to be restricted to archaeogastropods.

So-called bursicles (Szal, 1971) have been considered to be a synapomorphy of vetigastropods (Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988b: 398-399). However, bursicles have since been found also in several lepetelloid families (Haszprunar, 1988a; unpubl.), in the enigmatic *Melanodymia aurantiaca* Hickman, 1984 (cf. Haszprunar, 1989b), and in the seguenziids (Haszprunar, unpubl.). Whereas the latter can be reasonably included within the vetigastropods, lepetelloids and *Melanodymia* are still considered as outgroups. Up to now, bursicles have not been reported from any caenogastropod or heterobranch.

SUMMARY OF CHARACTER ANALYSIS

Summing up, the diagnosis of "an archaeogastropod" among the Gastropoda is:

- shell shape is a "symmetrical" limpet (no juvenile coiling);
- nacre is present;
- the protoconch is patellogastropod-like (lost with a part of the teleoconch by a septum), lepetelloid (embryonic shell apex fused with teleoconch), neritimorph (several largely overlapping whorls of larval shell), or trochoid-like (marine forms only);
- the adult shell muscle(s) is(are) paired;
- both ctenidia or osphradia or hypobranchial glands are retained;
- the ctenidia are bipectinate and supported by skeletal rods;
- both auricles are retained;
- both kidneys are retained;
- the rectum runs through the pericardium;
- ectaquatic or entaquatic fertilization by the "primitive" type of spermatozoa;
- the paired mesentoblast (4d-cell) is formed between the 63-cell and 64-cell stage, the formation of the prototroch occurs before or parallel of to this event and includes many cells;
- a docoglossate or rhipidoglossate radula type with massive cartilages is present;
- a radular diverticulum is present;
- oesophageal pouches are present;
- the "anterior loop" of intestine is present;
- a labial commissure is present;
- a streptoneurous and hypoathroid nervous system is present at least at the left side (THE ONLY DIAGNOSTIC CHARACTER);

- the eyes lack a cornea;
- a subradular organ is present;
- epipodial sense organs are present;
- bursicles are present.

With the single exception of the hypoathroid nervous system all characters listed above are valid but not diagnostic, meaning that there are archaeogastropods, which do not fulfill the specific requirement (Table 1). Because most characters listed are probably plesiomorphic (see Haszprunar, 1988b for reasoning), they also describe the gastropod archaetype (stem species or HAG = Hypothetical Ancestral Gastropod). In other words, the first gastropod was by definition an archaeogastropod.

"ARCHAEOGASTROPODA" A PARAPHYLETIC TAXON

MONOPHYLY OF ARCHAEOGASTROPODA

That archaeogastropod diagnostic characters are plesiomorphic strongly suggests that Archaeogastropoda is a paraphyletic taxon. This view is supported by the fact that the architaenioglossate groups (and certain trochoids?; cf. Healy, 1990) are linked by several characters, in particular by sperm morphology (see Healy (1988) for recent review), with the Caenogastropoda (Cerithioidea). If this is accepted, then the Archaeogastropoda in the given diagnosis cannot be clade. To decide between polyphyletic versus paraphyletic status the monophyly of Archaeogastropoda respectively of the Gastropoda as a whole has to be demonstrated.

Up to now very few people have doubted the holophyly (monophyly *sensu* Hennig, 1966) of the Gastropoda. The only group, for which a separation has recently been proposed, are the Patellogastropoda (cf. Golikov and Starobogatov, 1975; Shilenko, 1977):

However, all available evidence suggests that Patellogastropoda and all remaining gastropods have a common origin. The torsion process itself (cf. Crofts, 1955) as well as its various anatomical consequences (see review in Haszprunar, 1988b: 406) are essentially identical in all cases studied. Moreover, many peculiarities of the Patellogastropoda such as the symmetrical limpet shell, many shell muscle bundles, or shallow mantle cavity, are also present in the Cocculiniformia. Thus, the latter group links the Patellogastropoda with the remaining archaeogastropod groups. Finally, the shared condition of a hypoathroid nervous system, which does not depend on the torsion process, is an independent character supporting the common origin of Patellogastropoda and all remaining Gastropoda.

TABLE 1. Characters useful for a definition of Archaeogastropoda.

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Patellogastropoda	+	+	+	+	-	±	*	±	-	-	+	±	+	+	+	±	+	+	+	+	+	+	±	+	-	-	
Cocculinoidea	+	-	+	+	-	-	-	-	-	-	-	-	-	-	?	±	-	+	+	±	-	-	+	-	-	-	
Lepetelloidea	±	-	+	±	-	-	*	-	-	-	+	±	±	?	?	±	-	+	±	±	±	-	+	-	-	±	
Neritimorpha	-	-	+	±	-	-	±	+	-	±	-	±	-	-	?	+	±	+	+	+	+	-	+	-	-	-	
Melanodymia	-	+	+	-	-	-	-	+	-	-	-	-	-	?	?	+	-	+	+	+	-	-	+	*	-	+	
Peltoastroidea	-	+	+	±	-	-	-	+	+	-	±	-	-	?	?	+	-	+	+	+	+	-	+	*	+	-	
Neomphaloidea	-	+	+	-	-	-	-	+	+	-	-	-	-	?	?	+	-	+	+	+	+	-	+	*	-	-	
Scissurelloidea	-	-	+	+	+	+	±	±	+	+	+	+	+	+	?	+	-	+	+	+	+	±	+	-	-	+	
Lepetodriloida	-	+	+	+	-	+	-	+	+	+	+	+	-	?	?	+	-	+	+	+	+	-	+	*	-	+	
Fissurelloidea	-	-	+	+	+	+	+	±	+	+	+	+	±	+	?	±	-	+	+	+	+	+	+	-	+	+	
Haliotoidea	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	
Pleurotomarioidea	-	+	+	-	+	+	+	±	+	+	+	+	+	?	±	-	+	+	+	+	+	+	*	+	+	+	
Trochoidea	-	±	+	±	-	-	±	±	+	+	+	±	±	±	±	±	-	±	+	+	±	±	±	±	±	±	
Seguenzioidea	-	+	+	-	-	-	-	-	+	-	+	-	-	?	?	-	-	-	-	+	+	-	+	-	-	+	
Cyclophoroidea	-	-	*	-	-	-	-	*	*	-	-	-	-	-	?	-	-	-	-	-	+	-	+	-	-	-	
Ampullarioidea	-	-	*	-	-	-	-	-	+	-	-	-	-	-	*	-	-	-	-	-	+	-	+	-	-	-	
Caenogastropoda	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	±	-	-	-	-	-	
Heterobranchia	-	-	-	-	-	-	-	±	-	-	-	-	-	-	-	±	-	-	-	-	-	-	-	-	-	-	

Characters: (1) "symmetrical" limpet; (2) nacre; (3) archaeogastropod protoconch (see text for various types); (4) paired adult shell muscle(s); (5) paired ctenidia; (6) paired osphradia; (7) paired hypobranchial glands; (8) bipectinate gills; (9) skeletal rods in gill leaflets; (10) paired auricles; (11) two kidneys; (12) rectum runs through the pericardium; (13) fertilization is ect- or entaquatic; (14) "primitive" type of spermatozoa; (15) late formation of mesoentoblast, many trochoblasts; (16) docoglossate or rhipidoglossate-like radula type; (17) three or more pairs of radular cartilages; (18) radular caecum; (19) oesophageal pouches; (20) "anterior loop" of intestine; (21) pedal cords; (22) labial commissure; (23) streptoneurous and hypoathroid nervous system (see text for hypoathroid condition in heterobranchs); (24) open eyes; (25) subradular organ; (26) epipodial sense organs; (27) bursicles. Legend of characters: (+) present; (-) absent; (±) both conditions are present within the taxon; (*) no relevant data; (?) no data available.

MONOPHYLY OF HIGHER GASTROPODA

During recent years, general agreement has been reached in regarding the Caenogastropoda (the majority of former Mesogastropoda and the Neogastropoda) and the Heterobranchia (allogastropods and euthyneurans) as good clades. Disagreement exists, however, whether both clades have a common or a separate origin. Whereas Salvini-Plawen and Haszprunar (1987) and Haszprunar (1988b) claimed a common origin with the epiathroid nervous system as most important synapomorphy, Ponder (1991) favored an independent origin of the Heterobranchia out of the Archaeogastropoda. Also, a most recent computer-aided reanalysis of the subject (Ponder and Lindberg, 1992) is still equivocal in this respect.

Haszprunar (1988b) has proposed that the common ancestor of Caenogastropoda and the Heterobranchia probably was a large animal (centimeter-range) and showed larval planktotrophy. If so, the metatrochal ciliary bands of the veliger larva would be directly homologous in both groupings. Homology was also stated for the orthostrophic larval shell of the Caenogastropoda with the hyperstrophic larval shell of the Heterobranchia. In contrast, Ponder (1991) assumed a small (millimeter-range) heterobranch stem species with lecithotrophic development and an independent evolution of larval planktotrophy and of the larval shell in Caenogastropoda and Heterobranchia.

Several indices support the monophyletic version: (1) The lecithotrophic heterobranchs show a more or less distinct larval shell, at least their protoconchs always show more than one whorl, calling for a planktotrophic ancestor; (2) Fossil omalogyrids and orbitestellids are lecithotrophic or planktotrophic (Bandel, 1988a, 1991); (3) Both groups, Caenogastropoda and Heterobranchia (opisthobranchs were investigated) have metatrochal ciliary bands with the so-called "discoidal reticulate lamellae", a specific type of glyco-cocalix (Bonar and Maugel, 1982). This structure is lacking in the metatrochi of bivalvian planktotrophic larvae and in "trochophore-like" planktotrophic larvae of other spiralian phyla. Unfortunately the presence or absence of discoidal reticulate lamellae could not yet be established in the planktotrophic Neritidae. Nevertheless, this highly specific and complex structure calls for direct homology of metatrochi in Caenogastropoda and Heterobranchia and thus for common origin of larval planktotrophy in both groups; (4) Also the mentioned spatio-temporal shifts in the formation of the mesentoblast and the prototroch call for a common origin; (5) Finally, "the significant number of spermiogenic features shared by Caenogastropoda and Heterobranchia suggests either that these two groups arose from a common 'archaeogastropod' source possessing these features or that heterobranchs were derived from early caenogastropods" (Healy, 1993b).

On the other hand, recent investigations on the osphradial fine-structure of *Campanile symbolicum* Iredale, 1917 (cf. Haszprunar, 1992b) have revealed that this enigmatic relict species should no longer be regarded as a link between primitive caenogastropods and heterobranchs as previously suggested (Haszprunar, 1988b), but should be classified as the earliest offshoot among the Caenogastropoda. The same conclusions has been reached independently by spermatological investigations on a related family, Plesiotrochidae (Healy, 1993a).

In addition, the discovery of primitive heterobranchs with rhipidoglossate radula (Hyalogyrinidae; see above) seem to support Ponder's (1991) view, although a distinct archaeogastropod sister-group cannot be established at present (Haszprunar, in prep.).

“ARCHAEOGASTROPODA” IN CLASSIFICATION

So far the conclusion has been reached that Archaeogastropoda is a paraphyletic taxon, from which one or two lines (Caenogastropoda and Heterobranchia) have evolved (see above). There is a long-lasting debate in systematics, whether or not paraphyletic taxa should be allowed in phylogenetic classifications (i.e. unequivocal retranslation in the basic cladogram is possible; Wiley, 1981).

Starting from the cladistic point of view (no paraphyletic groups), what would be the alternatives?: The holophyly of Patellogastropoda and of Neritimorpha is well established by synapomorphies (Haszprunar, 1988b), and certain authors even regard them as distinct orders out of Archaeogastropoda (e.g. Lindberg, 1988; Bandel, 1992). Holophyly of Cocculiniformia is more difficult to establish (Haszprunar, 1988a, b), but also this group might be excluded as an order proper. Although there is not a single autapomorphy known for a taxon Architaenioglossa, holophyly cannot be ruled out, and the taxon has a long tradition. The real problem are the remaining groups (*Melanodrymia*, Neomphaloidea, Peltospiroidea, Vetigastropoda, Seguenzioidea). To these groups several new ones such as the Pendromidae (cf. Warén, 1991; synonym Trachysmatidae Thiele, 1925) are or will be added in the near future. Such a taxon “Archaeogastropoda” is probably again a paraphyletic assemblage, and (even more serious) no distinct diagnosis can be given for a uniting taxon.

Hickman (1988) proposed to replace Vetigastropoda (zeugobranchs, Lepetodrilioidea, Trochoidea, probably also Seguenzioidea due to their recently found bursicles and epipodial sense organs) by Archaeogastropoda. But if so, what to do with the remaining groups? In other words: A restricted use of Archaeogastropoda does not solve any of the above mentioned problems, but adds the major one of a lacking diagnosis. Therefore I don't think that abolishment

or a restricted use of Archaeogastropoda is helpful.

Hennig (1966, 1974) mentioned two main reasons to abolish paraphyletic groups. (1) His main argument, the equal use of para- and holophyletic taxa leads to serious confusion about the basic cladogram, is still fully valid. However, already Wiley (1981) mentioned in his Rule 1: “Taxa classified without qualification are monophyletic *sensu* Hennig (1966). Non-monophyletic groups can be added, if they are clearly qualified as such”. As outlined by the author (Haszprunar, 1986, 1990) a specific marking of paraphyletic groups and a general sequential arrangement of subtaxa overcomes Hennig's (1966) main argument.

Hennig's (1974) second argument, that paraphyletic groups are some kind of polyphyletic group, must be rejected: In contrast to polyphyletic taxa, paraphyletic groups have a common ancestor (are monophyletic *sensu lato*) and represent like holophyletic (monophyletic *sensu stricto*) taxa a continuous genealogical line.

The case of Archaeogastropoda also clearly demonstrates that a paraphyletic group is not by definition defined by a “lack of x” characters, but by positive characters, which are nevertheless plesiomorphic (see summary of character analysis).

The final cladistic argument, that only holophyletic taxa are “natural entities” and that paraphyletic groups are “arbitrary constructions” is rejected on following reasons: (1) Classification does not concern a group or its phylogeny itself, but a reconstruction of phylogeny, the nature of which is always hypothetical and probabilistic. According to Darwin (1872) “natural” means “strictly genealogical” (see also Wiley, 1981: rule 1); this requirement is fulfilled by the marked use of paraphyletic groups. (2) All paraphyletic groups once were holophyletic, meaning that they included all their descendents. Until the descent of Caenogastropoda and Heterobranchia “Archaeogastropoda” in the given definition was a holophyletic group.

The use of marked paraphyletic taxa has a number of additional advantages (cf. Haszprunar, 1986, 1990): (1) More stability: many traditional or even nomenclatorically conserved (genera, species) paraphyletic taxa such as “Archaeogastropoda” can be still used in a phylogenetic system, if they are clearly marked. (2) So-called “chronospecies” such as (+) “*Homo erectus*” can be expressed unequivocally and clearly distinguished from offshoots such as (+) *Homo sapiens neanderthalensis*. (3) Combination of Wiley's (1981) *sedis mutabilis* and the marking of paraphyletic taxa enables clear expression of so-called “metataxa” (cf. Gauthier, 1986: i.e. holo- or paraphyletic) such as in the case of “Architaenioglossa” with Ampullarioidea and Cyclophoroidea both with *sedis mutabilis* (s. Haszprunar, 1988b).

In the case of “Archaeogastropoda” an additional

argument can be made in favor of its marked retention: there are numerous species and groups, extinct or recent (e.g. *Pendromidae* or *Adeuomphalus* and *Palazzia*; cf. Warén, 1991), where conchological or radular or morphological evidence clearly allows their inclusion among the archaeogastropods in the given definition, but where classification within one of the subgroups cannot yet be established. Retaining "Archaeogastropoda" as a formal taxon allows a much clearer defined "pot" for such forms.

Summing up, I recommend the retention of "Archaeogastropoda" as a formal taxon in gastropod classification (cf. Haszprunar, 1988b). The given definition, which is mainly based on protoconch and neural characters, is valid for most extinct and recent forms. However, as expressed by its marking: have in mind that "Archaeogastropoda" is not a clade but a paraphyletic taxon. In fact, "Archaeogastropoda" is the stem group of the Gastropoda, yet it shows the widest secondary radiation of all gastropod groups.

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